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A review and updated classification of pollen gathering behavior in bees (Hymenoptera, Apoidea)

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Abstract

Pollen is the primary protein and nutrient source for bees and they employ many different behaviors to gather it. Numerous terms have been coined to describe pollen gathering behaviors, creating confusion as many are not clearly-defined or overlap with existing terms. There is a need for a clear yet flexible classification that enables accurate, succinct descriptions of pollen gathering behaviors to enable meaningful discussion and comparison. Here, we classify the different pollen gathering behaviors into two main classes: active and incidental pollen collection. Active pollen collection is subdivided into six behaviors: scraping with the extremities, buzzing, rubbing with the body and/or scopae, rubbing with the face, tapping, and rasping. In addition to the active and incidental pollen gathering behaviors, many bees have an intermediate step in which they temporarily accumulate pollen on a discrete patch of specialized hairs. Each behavior is described and illustrated with video examples. Many of these behaviors can be further broken down based on the variations found in different bee species. Different species or individual bees mix and match these pollen collecting behaviors depending on their behavioral plasticity and host plant morphology. Taken together, the different behaviors are combined to create complex behavioral repertoires built on a foundation of simple and basic steps. This classification sets the groundwork for further research on various topics, including behavioral plasticity in different species, comparisons between generalists and specialists, and the relative effectiveness of different pollen gathering behaviors.

Keywords

Pollinators, pollen collection, foraging behavior, floral specialization, oligolecty, floral hosts, Anthophila

Introduction

Bees visit flowers primarily for nectar and pollen, which they use as provisions for their young and to meet their own energetic and nutritional requirements (Michener 2007; Cane et al. 2016). Pollen is the primary resource in the larval provisions of most species, and bees have evolved behaviors to efficiently collect large amounts of pollen (Thorp 2000). Unsurprisingly, not all bees gather pollen identically, and many different pollen gathering behaviors exist. For example, even on the same floral host, different bee species often use different pollen gathering behaviors (Thorp 1979). In addition, flexibility exists at the individual level, with individual bees using different pollen gathering behaviors depending on the floral host and pollen availability (Heinrich 1976b; Prosi et al. 2016; Russell et al. 2017). The types of behavior that bees use can influence their floral preferences and may impact their effectiveness as pollinators. Due to the importance of pollen gathering behavior and the growing interest in bee biology and pollination ecology, the number of research articles that describe or mention pollen gathering behavior has grown rapidly. As a result, it is necessary to produce a standardized terminology which both accurately describes the different behaviors and facilitates their effective communication.

Pollen-gathering behavior in bees has historically been divided into two main types: active and incidental (or passive) collection (Parker 1926; Doull 1970; Inouye et al. 1994; Westerkamp 1996; Thorp 2000). Active pollen collection refers to the purposeful uptake of pollen, generally through the use of the forelegs and mandibles, directly from anthers or other floral surfaces. Incidental (or passive) pollen collection refers to pollen that accumulates on bees as they forage for nectar – this pollen may either be packed into the pollen transporting structures or groomed and discarded (Doull 1970). However, such broad categories oversimplify the diversity of pollen gathering behaviors exhibited by bees and the line between active and incidental pollen collection is often unclear. Previous researchers have broken down active pollen gathering into numerous variants, but these attempts typically lack a broader framework and conflate, or overlap with, existing definitions. For example, a single species – *Osmia montana* Cresson (Megachilidae) – has had its pollen gathering behavior variously coined as "thumping," "tapping," "patting," and "drumming" (Rust 1974; Cripps and Rust 1989; Cane 2011; Cane 2017). Conversely, the same term can have multiple meanings, such as "scrabbling," which has been variously used to describe bees that scrape with the forelegs or run over a plane of flowers (Percival 1955; Thorp 2000). These numerous, overlapping, and poorly-defined terms illustrate the need for more precise and consistent terminology to describe pollen gathering behavior.

While pollen gathering behavior has previously been reviewed by others, these works tend to focus on such disparate fields as the phenological, chemical, and morphological adaptations of bees to flowers (Müller 1996b; Thorp 1979, 2000). In addition, the recent proliferation of high-speed, high-definition video technology enables the efficient study and communication of previously inaccessible or complex behaviors. Here, we build on the existing schema of active vs. incidental pollen gathering and propose a comprehensive terminology to categorize and describe the full range of pollen-gathering behaviors. Active pollen gathering is broken down into six types,

which can be further subdivided based on the nuances of particular bee groups and the morphology of floral hosts. Our updated classification systematizes pollen gathering behavior and facilitates the description and communication of behavioral observations. In addition, it provides a platform to better address questions on the breadth, limitations, evolution, and convergence of pollen gathering behaviors.

Methods

Pollen gathering videos were recorded by ZMP and MCO as well as gathered from other researchers or sources (e.g. youtube.com) and used with permission. To record behavior, we used a Sony A65 with a 90mm macro lens and a Pentax Optio WG-2. Scanning electron microscope images were taken with a Quanta FEG 650 Scanning Electron Microscope. Morphological terminology generally follows Michener (2007); as exceptions for accessibility, abdomen is used to refer to the metasoma and thorax is used to refer to the mesosoma. Classification generally follows Michener (2007) except eucerines follow Dorchin et al. (2018). Bees were identified using either collected specimens or still images from videos.

We broadly surveyed the literature for descriptions of pollen gathering behavior. We combined keyword searches in google scholar with manual searching of older literature from the literature collection of the Pollinating Insect Research Unit. Selecting appropriate terminology proved difficult because every pollen gathering behavior has been referred to by multiple different terms. In general, three main considerations were taken into account in selecting the most appropriate terminology for the different pollen gathering behaviors: priority (first known instance of use), usage (prevalence of a term in the scientific and popular literature), and accuracy (how well a term describes a given behavior). Exceptions were made for usage and accuracy, particularly when terms had conflicting or multiple meanings, or when a particular usage is widely accepted.

Results and discussion

Types of pollen gathering behavior

We define pollen gathering behaviors as the movements that bees use to acquire, actively or incidentally, pollen from anthers or other pollen presenting structures. Pollen gathering is related to, but separate from, pollen transport, which refers to the carrying of accumulated pollen back to the nest in specialized transport structures (Roberts and Vallespir 1978; Portman and Tepedino 2017). The different pollen gathering behaviors (listed below) may be used individually or in combination, concurrently or sequentially, creating complex repertoires from a set of simple, well-defined building blocks. Taken together, our definitions offer a useful guide to the full set of major behaviors used by bees when gathering pollen.

In foraging from flowers, bees have three possible primary purposes on each trip: to acquire nectar (or oil), pollen, or both. We term pollen gathering **active** when pol-

len is the primary objective or when nectar (or oil) and pollen are co-objectives. Active pollen gathering is broken down into six pollen gathering behaviors as described below. We term pollen gathering **incidental** when nectar is the primary objective and pollen is passively accumulated on the body. The bee then "decides," based on pollen and floral characteristics, and on need, to discard or keep the pollen. Bees may also incidentally collect pollen on non-target areas of the body while actively gathering pollen. Such pollen may or may not be gathered into the pollen transporting structures.

Active pollen gathering behaviors can be broken up into six types, listed loosely in order of prevalence:

- **Scraping with the extremities:** use of the legs or mouthparts to remove pollen directly from anthers, or, less commonly, to glean pollen from flowers.
- **Buzzing:** use of the flight muscles to vibrate a flower to assist with pollen release.
- **Rubbing with the body and/or scopa(e):** the gathering of pollen through direct and more or less continuous contact with the anthers by the main trunk of the body (thorax, abdomen) and/or the scopal hairs.
- **Tapping:** picking up pollen from anthers by a rapid up and down motion of the abdominal venter.
- **Rubbing with the face:** continuous and more or less direct contact with the anthers by the face.
- **Rasping:** rubbing of the thoracic dorsum against anthers, causing the anthers to vibrate and release the pollen.

Incidental pollen gathering (not broken down into types): the use of pollen that has accumulated on the body either through nectar gathering or on non-target areas as a result of a primary pollen gathering behavior. A major component of incidental behavior is the degree of movement by the bee, which influences the amount of pollen that adheres to the bee through contact.

Scraping with the extremities

Scraping with the extremities refers to the use of the legs and/or mouthparts (including biting with the mandibles) to gather pollen with a repetitive unidirectional motion (Figure 1; Suppl. material 1). The term "scraping" is generally accepted by most authors, though other terms, such as "brushing," "raking," "scrabbling," "stroking," and "wiping," have also been used (Casteel 1912; Jander 1976; Michener et al. 1978; Thorp 1979, 2000). Scraping can be performed with the forelegs, midlegs, hindlegs, mandibles, mouthparts, or combinations of these appendages, making it important to specify which are used and the manner of their use. Indeed, scraping with the extremities is something of a catchall category, and it could reasonably be divided into multiple distinct types. However, the diversity of behaviors, combined with the relative lack of detailed descriptions, made it infeasible to clearly and consistently split the category further.

Figure 1. *Andrena chlorogaster* Viereck (Andrenidae) biting with the mandibles and scraping with the forelegs **A** foreleg extended and **B** foreleg scraping towards the body. Note that the bee is also scraping the pollen from anthers by biting with the mandibles.

Scraping pollen directly from the anthers or other pollen-presenting structures with the basitarsal brushes of the forelegs is the most common pollen gathering method used by bees (Grinfel'd 1962; Michener et al. 1978; Westerkamp 1996; Michener 2007). The forelegs and mandibles are used together to scrape pollen, though the midlegs and/or hindlegs may also be used. The most typical form of the behavior is described in detail for *Lasioglossum zephyrum* (Smith) (Halictidae) (Batra 1966) and *L. lusorium* (Cockerell) (Bohart and Youssef 1976). The forelegs may also be used to glean pollen from other surfaces, such as flower petals, or even the scopae of other bees (termed "cleptolecty;" Thorp and Briggs 1980, Snelling and Stage 1995). One variation is seen in bees which "strike" poricidal anthers with the forelegs to loosen pollen. Striking has been observed in *Ptiloglossa* on *Solanum* (Linsley 1962), *Osmia ribifloris* Cockerell on blueberry (Torchio 1990), and *Apis mellifera* L. (Apidae) on cranberry ("drumming," Cane et al. 1993).

One term that refers to scraping with the forelegs – "scrabbling" – is particularly problematic because it has apparently adopted two different meanings. In the original, and most well-accepted usage, it refers to scraping with the forelegs and mandibles (Percival 1955; Harper 1957). However, scrabbling has also been defined as a more specific behavior whereby bees (and honey bees in particular) scrape with their forelegs and mandibles while *simultaneously* running across a plane of flowers (Doull 1970; Thorp 2000). Currently, scrabbling is almost exclusively used in the former sense, to refer only to scraping with the forelegs and mandibles (e.g. Cane and Dunne 2014; Muth et al. 2016; Russell et al. 2017). As a result of this confusion, the term scrabbling should either be avoided or explicitly paired with descriptions of the degree of movement.

The mouthparts are also frequently used to gather or loosen pollen. The mandibles are most often used to bite anthers to loosen the pollen in tandem with scraping with the forelegs (Sladen 1912; Thorp 1979), though some bees hang on by the mandibles while gathering with the forelegs (e.g. Batra 1966). Some bees, including *Apis*, *Colletes* (Colletidae) (Buchmann et al. 1977), *Bombus* (Apidae) (Todd 1882; Robertson 1890; Bowers 1975), and various halictines (Thorp and Estes 1975), use the mandibles in a

"milking" motion to gather pollen from poricidal flowers, such as *Cassia* (Fabaceae) and *Solanum* (Solanaceae) (however, the observations of *Bombus* from the late 1800's may be misinterpretations of buzzing behavior). This behavior is often combined with buzzing to release pollen (Thorp and Estes 1975). The mandibles can also be used to chew open anthers to render the pollen more accessible, a behavior observed in *Lasioglossum lustrans* (Cockerell) (Estes and Thorp 1975) and repeatedly in *Trigona* (Apidae) (Wille 1963; Inouye 1980; McDade and Kinsman 1980; Renner 1983, Telles et al. 2018).

The midlegs are generally used to assist the forelegs in scraping pollen (Westerkamp 1996). However, some megachilid bees have specialized hair brushes on the femur of the middle and/or hind legs that appear to be used to scrape pollen from Asteraceae flowers (Müller and Bansac 2004). Although the exact pollen gathering movements remain unclear, the mid or hind legs appear to bend at the femoral-tibial joint to scrape pollen from individual anthers, mirroring the movements used to groom pollen off the foreleg by the midleg (ZP, pers. obs).

Scraping movements are also made with the hind legs, particularly on keel-shaped flowers. In these cases, the hind legs appear to be used because the front and middle legs are occupied in obtaining purchase and spreading the wing petals to expose the anthers. Various *Andrena* (Andrenidae), *Anthophora* (Apidae), *Apis*, *Bombus*, and megachilids use these behaviors on keel-shaped flowers such as *Collinsia* (Plantaginaceae) and *Lupinus* (Fabaceae) (Rust and Clement 1977; Wainwright 1978). One particularly interesting example is *Samba turkana* Packer (Melittidae), which uses an enlarged and curved hind tibial spur to scrape pollen from anthers of *Crotalaria* (Fabaceae) (Packer and Martins 2015).

In bees that gather pollen primarily by rubbing with the body and/or scopae (discussed in a later section), the hind legs are often used in an accessory fashion to gather a clump of anthers and draw them to the body, as well as to help scrape pollen from the gathered anthers. This gathering and scraping behavior is seen in Megachilidae such as *Osmia cornuta* (Latreille) (Monzón et al. 2004) and *O. lignaria* Say (Rust and Clement 1977). It should be noted that scraping with the hind legs is distinct from rubbing with the scopae, which are often located on the hind legs. Scraping with the hind legs entails removal of pollen from anthers with a repeated, unidirectional movement where the pollen is then packed into another structure. In contrast, rubbing with hindleg scopae involves rubbing the scopal hairs back and forth on the anthers, and the continuous contact with the pollen works the pollen directly into the scopal hairs.

Bees that scrape with the extremities often possess morphological features that improve their efficiency. Many examples of hooked hairs on the forelegs and especially the foretarsi are associated with specialization on flowers with narrow corollas (Thorp 1979), although exceptions to the narrow-corolla association exist (Neff 2004). Examples have been reviewed by Thorp (1979, 2000); more recent examples include two species of European *Colletes* on hosts in Boraginaceae (Müller and Kuhlmann 2003), multiple species of North American *Colletes* on various hosts (Neff 2004), and multiple *Hoplitis* (Megachilidae) on various hosts (Sedivy et al. 2013).

Similar to the forelegs, the mouthparts (primarily the stipes, galea, and labial and maxillary palpi) can be modified, often with hooked hairs, to extract pollen from flowers

with narrow corollas. The presence and use of modified hairs on the mouthparts have been reviewed by Thorp (1979, 2000). More recent examples include various apid and halictid visitors to Pontederiaceae (Alves-dos-Santos 2003), *Ceblurgus longipalpis* Urban and Moure (Halictidae) on *Cordia* (Boraginaceae) (Milet-Pinheiro and Schlindwein 2010), multiple *Anthophora* on various hosts (Orr et al. 2018), *Haetosmia vechti* (Peters) (Megachilidae) on *Heliotropium* (Boraginaceae) (Gotlieb et al. 2014), and multiple Palaearctic *Hoplitis* on various hosts (Müller 2006; Sedivy et al. 2013). In addition to modified hairs, other bees have enlarged or elongated labial palpi, but it is not clear whether the function is to assist in the removal of pollen or the sucking of nectar. Examples include *Perdita heliotropii* Cockerell (Andrenidae), a specialist on *Heliotropium* (Timberlake 1958), and *Hesperapis* sp. (Stage manuscript name *"palpalis"*) (Melittidae), a specialist on Polemoniaceae (Stage 1966).

Buzzing

Buzzing, commonly referred to by the suboptimal terms "buzz pollination" and "floral sonication," is the use of the thoracic flight muscles to generate audible vibrations that aide in accessing and collecting pollen from a flower (Figure 2; Suppl. material 2; Buchmann 1983; Thorp 2000). Buzzing induces the release of pollen from the anthers, which the bee usually receives on the venter, where the adhesion of pollen is aided by the electrostatic attraction of the pollen to the bee's body and hairs (Buchmann and Hurley 1978; Corbet et al. 1982; Buchmann 1983; Vaknin et al. 2000). The legs are subsequently used to groom pollen from the body into the pollen transporting structures. A variant of buzzing, "buzz milking" (Cane and Buchmann 1989), is performed by *Protandrena mexicanorum* (Cockerell) (Andrenidae), which buzzes anthers of *Solanum* while gradually sliding up the upward-facing anthers before curling over the tips of the anthers to receive pollen. Another variant of buzzing, described as "head-banging," has been recorded for *Amegilla murrayensis* (Rayment) (Apidae), which repeatedly taps its head against anthers while buzzing rather than gripping with the mandibles (Switzer et al. 2016). Finally, buzzing can also be used in combination with rubbing with the face (Müller 1996a).

Here, we focus primarily on terminology because the extent and occurrence of buzzing behavior has been reviewed by others (see Buchmann 1983; Thorp 2000; Cardinal et al. 2018). Although it is clear what buzzing refers to, many different terms have been used to describe it (Table 1). Observations of buzzing have been made since at least 1902 (e.g. Lindman 1902; Schrottky 1908; Plath 1934; Rayment 1944; Meidell 1944; Osorno-Mesa 1947; Rick 1950; see Teppner 2018 for a discussion on the earliest mention), but it remained little-known and poorly-defined until Michener (1962) and Wille (1963) described the behavior in-depth and referred to it as "buzzing." Buchmann (1974, 1983) later codified the term "buzz pollination," though he and others have often used alternative terminologies, often within a single paper (Table 1). Starting in 1985, the term "floral sonication" has also been used to refer to this behavior (Cane 1985; Cane et al. 1985), though this term is a misnomer since me-

Figure 2. *Bombus impatiens* Cresson (Apidae) buzzing a *Solanum* (Solanaceae) flower. The pulsed vibrations expel the pollen from the anthers. Image adapted from Russell et al. (2016)

chanical vibrations, rather than sound waves, cause the pollen to be expelled. Due to their priority (Michener 1962; Wille 1963; Buchmann 1983) and widespread usage, we recommend using the term buzzing to refer broadly to the behavior, and variants of "buzz" (e.g. "buzzed," "buzzes") to refer to the specific act of buzzing flowers. Despite its wide usage, we do not recommend the term "buzz pollination" because it is also a misnomer as it does not necessarily effect pollination as the name implies. Others have proposed using the term "vibratile pollen harvesting" or "vibratory pollen collection" as these descriptive terms are more technically correct than "buzz pollination," but these terms have not been widely adopted (Neff and Simpson 1988; Teppner 2018).

Members of all bee families have been documented using buzzing behavior, though it is uncommon or rare in Andrenidae, Melittidae, and Megachilidae (Meidell 1944; Buchmann and Hurley 1978; Buchmann 1983; Houston and Thorp 1984; Cane et al. 1985; Neff and Simpson 1988; Thorp 2000). Interestingly, some of the most generalized bees, such as honey bees and *Trigona* spp., do not buzz flowers (Buchmann 1983; King and Buchmann 2003; Michener 2007). Although bees buzz a wide variety of plants (>72 families, reviewed in Buchmann 1983), this behavior was traditionally considered exclusive to plants with poricidal, or hidden, anthers (Michener 1962). However, there are many exceptions to this, and bees buzz a variety of flowers in the families Asteraceae, Cucurbitaceae, Fabaceae, Papaveraceae, Rosaceae, Plantaginaceae, and others (e.g. Suppl. material 2; Heinrich 1976a; Buchmann 1985; Bernhardt 1989; Russell et al. 2017).

Rubbing with the body and/or scopae

Rubbing with the body and/or scopae refers to the use of direct, more or less continuous contact between the anthers and the scopae and/or venter of the main body segments (thorax or abdomen). The defining character of rubbing with the body and/

Table 1. Terminology used to refer to buzzing in the literature. This list is not comprehensive; instead, it focuses on the first usage of terms and major works on buzzing.

Term used	Genus or Species	Floral Host	Citation
"einer gewaltsamen Vibration des Insektenkörpers und zugleich der ganzen Blüte" [a violent vibration of the insect body and at the same time the whole flower]	*Bombus* (Apidae)	*Senna* (Fabaceae)	Lindman 1902 (see Teppner 2018)
"die Bienen … versetzen die Blüte in starke Vibration, so dass der Pollen aus den Antheren herausgeschüttelt" [the bees… cause the flower to vibrate strongly, causing the pollen to be shaken out of the anthers]	*Augchlora* (Halictidae), *Oxaea* (Andrenidae), *Ptiloglossa* (Colletidae), *Xylocopa* (Apidae)	*Senna*, *Physalis* (Solanaceae), *Solanum* (Solanaceae)	Schrottky 1908 (see Teppner 2018)
"the worker seizes the anthers with her mandibles and first two pairs of legs, and shakes them, emitting an impatient buzz, as if angry because the stamens do not give up their pollen at once"	*Anthophora* (Apidae), *Bombus*	*Rosa* (Rosaceae), *Rubus* (Rosaceae)	Plath 1934
"vigorous whirrings" and "whirring method"	*Bombus*, *Megachile* (Megachilidae)	*Melampyrum* (Orobanchaceae)	Meidell 1944 (posthumously published notes)
"while…collecting pollen…she makes the continuous sound that has been compared with that of a honey-bee caught in a spider's web"	*Amegilla* (Apidae)	Not specified	Rayment 1944
"vibrar las anteras" ["vibrates the anthers"]	*Bombus*, *Xylocopa*	Not specified	Osorno-Mesa 1947
"vibrating the flowers with rapid leg movements accompanied by a high pitched hum"	Not specified	*Solanum* [as *Lycopersicon*] (Solanaceae)	Rick 1950
"buzz," "buzzing," "buzzing behavior," and "vibrate"	Various Andrenidae, Apidae, and Halictidae	*Cassia* (Fabaceae), *Solanum*	Michener 1962
"buzzing," "buzzing behavior," and "buzzing technique"	Various Apidae, Colletidae, and Halictidae	*Cassia*	Wille 1963
"vibrate the anthers"	Various Apidae, Andrenidae, and Colletidae	*Solanum*	Linsley and Cazier 1963
"vibratory pollen collection" and "wing vibration"	*Bombus*, various Halictidae	*Dodecatheon* (Primulaceae)	Macior 1964
"buzz," "buzzing," and "buzzing behavior"	*Agapostemon* (Halictidae)	*Chamaecrista* (Fabaceae), *Solanum*	Roberts 1969
"buzzed the anthers" and "vibrate the anthers"	*Caupolicana* (Colletidae), *Ptiloglossa*	*Datura* (Solanaceae), *Solanum*	Linsley and Cazier 1970
"vibrate their wings"	*Bombus terricola* Kirby	*Solanum*, *Spiraea* (Rosaceae)	Heinrich 1972
"buzz (vibratile) pollination," "buzzing," and "buzzing technique"	*Centris* (Apidae), *Melipona* (Apidae)	*Senna* [as *Cassia*]	Buchmann 1974
"vibratory behavior" and "vibrated anthers"	Various Apidae and Halictidae	*Chamaecrista* [as *Cassia*]	Thorp and Estes 1975
"vibration of the thorax"	*Anthophora*, *Augochlorella* (Halictidae), *Bombus*, *Psaenythia* (Andrenidae), *Xylocopa*	*Solanum*	Bowers 1975
"buzz," "buzzing," and "vibrated the anthers while emitting a buzzing sound"	*Bombus*	*Rosa*, *Solanum*, *Vaccinium* (Ericaceae)	Heinrich 1976b
"buzz," "buzz pollination," "buzzing," "buzzing behavior," and "vibratile pollination"	*Anthophora*, *Bombus*, *Colletes*, *Xylocopa*. Also, *Volucella* (Syrphidae)	*Solanum*	Buchmann et al. 1977
"buzz," "'buzz' pollination," "buzzing," "shivering," "vibratile pollination," and "vibrational pollination"	Not specified	*Solanum*	Buchmann and Hurley 1978
"wing vibration" and "wing vibration method"	*Bombus*	*Echeandia* (Asparagaceae)	Bernhardt and Montalvo 1979
"buzz pollination," "buzzing," "buzzing behavior," and "vibratory behavior,"	Not specified	Not specified	Thorp 1979
"buzzing" and "vibratile behavior"	Not specified	Not specified	Eickwort and Ginsberg 1980
"high frequency wing vibrations" and "vibrating"	*Bombus*	*Pedicularis* (Orobanchaceae)	Laverty 1980

Term used	Genus or Species	Floral Host	Citation
"buzz pollination," "buzzing," "floral vibration," "vibratile pollination," and "vibratile technique"	*Euglossa* (Apidae), *Paratetrapedia* (Apidae)	*Mouriri* (Melastomataceae)	Buchmann and Buchmann 1981
"buzz," "buzz pollination," "buzzing behavior," "buzzing, "vibratile pollen harvesting," "vibratile manipulation," "vibrational pollination," "vibrating," and "floral vibration"	Various Apidae, Andrenidae, Colletidae, Halictidae, Melittidae	Various plant families	Buchmann 1983
"thoracic vibration" and "vibrate"	*Lasioglossum* (Halictidae)	*Hibbertia* (Dilleniaceae)	Bernhardt et al. 1984
"buzzing technique"	Stenotritidae	Not specified	Houston and Thorp 1984
"buzz-pollination" and "floral sonication"	*Bombus*	"poricidally dehiscent, nectar-free flowers"	Cane 1985
"buzz," "buzz pollination," "buzz or vibratile pollen foraging" "buzzing," "buzzing behavior," "floral buzzing," and "floral sonication"	*Bombus*, *Melitta americana* (Smith) (Melittidae)	*Vaccinium*	Cane et al. 1985
"buzz," "buzz pollination," "buzzing," "buzzing behavior," "floral buzzing," "floral vibration," "vibratile methods," "vibratile pollen-collecting behavior," "vibratile pollen harvesting," "vibratile foraging behavior," "vibrating," "vibratory pollen-collecting behavior," "vibratory manner," and "vibratory pollen harvesting"	*Bombus*, *Eucera* [as *Xenoglossa*] (Apidae), *Megachile*, *Xylocopa*	Asteraceae, Cucurbitaceae, Papaveraceae, Rosaceae, Scrophulariaceae	Buchmann 1985
"buzz," "buzz pollination," "buzzing," and "vibratory pollen collection"	*Bombus*	*Actinidia* (Actidiniaceae), *Borago* (Boraginaceae), *Polygonatum* (Asparagaceae), *Symphtum* (Boraginaceae)	Corbet et al. 1988
"buzz," "buzzing," and "sonicate"	*Bombus*, *Habropoda* (Apidae)	*Vaccinium*	Cane and Payne 1988
"thoracic vibration," "vibratile behavior," and "vibratile pollen-harvesting"	*Megachile*	*Chamaecrista*	Neff and Simpson 1988
"buzz," "buzz-harvesting," "buzz-milking," "buzz pollination," "buzzing," and "sonicate"	*Protandrena mexicanorum* (Cockerell) (Andrenidae)	*Solanum*	Cane and Buchmann 1989
"buzz," "buzzing," "floral sonication," "sonicate," and "vibratile buzzes"	*Bombus*, *Ptiloglossa*	*Solanum*	Buchmann and Cane 1989
"buzzing," "buzz-collection"	Various	Various	Roubik 1989
"buzzing"	Not specified	Not specified	Westerkamp 1996
"floral sonication" and "sonicate"	Not specified	Not specified	Wcislo and Cane 1996
"buzz," "buzz pollination," "buzzing," "buzzing behavior," "sonication," "sonication behavior," "vibratile or buzz pollination," and "vibrating"	Various Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae, and Stenotritidae	Various floral hosts	Thorp 2000

or scopae is the curling of the abdomen, which generally moves in an up and down motion, or less often, a back-and-forth or telescoping motion (Figure 3; Suppl. material 3). This type of pollen gathering is here used in a broader sense than generally recognized by previous authors who largely restricted the definition to eucerine bees on sunflowers (e.g. Cane 2017). There are two variants of this behavior that depend on whether the scopae are located on the abdominal venter or the hind legs. Bees that transport pollen in abdominal scopa gather pollen directly into the scopal hairs, whereas bees that transport pollen with hind leg scopae must transfer pollen from the venter into the scopae. Despite this difference, the general pollen gathering movements are largely the same, and further, many bees straddle these categories because they have

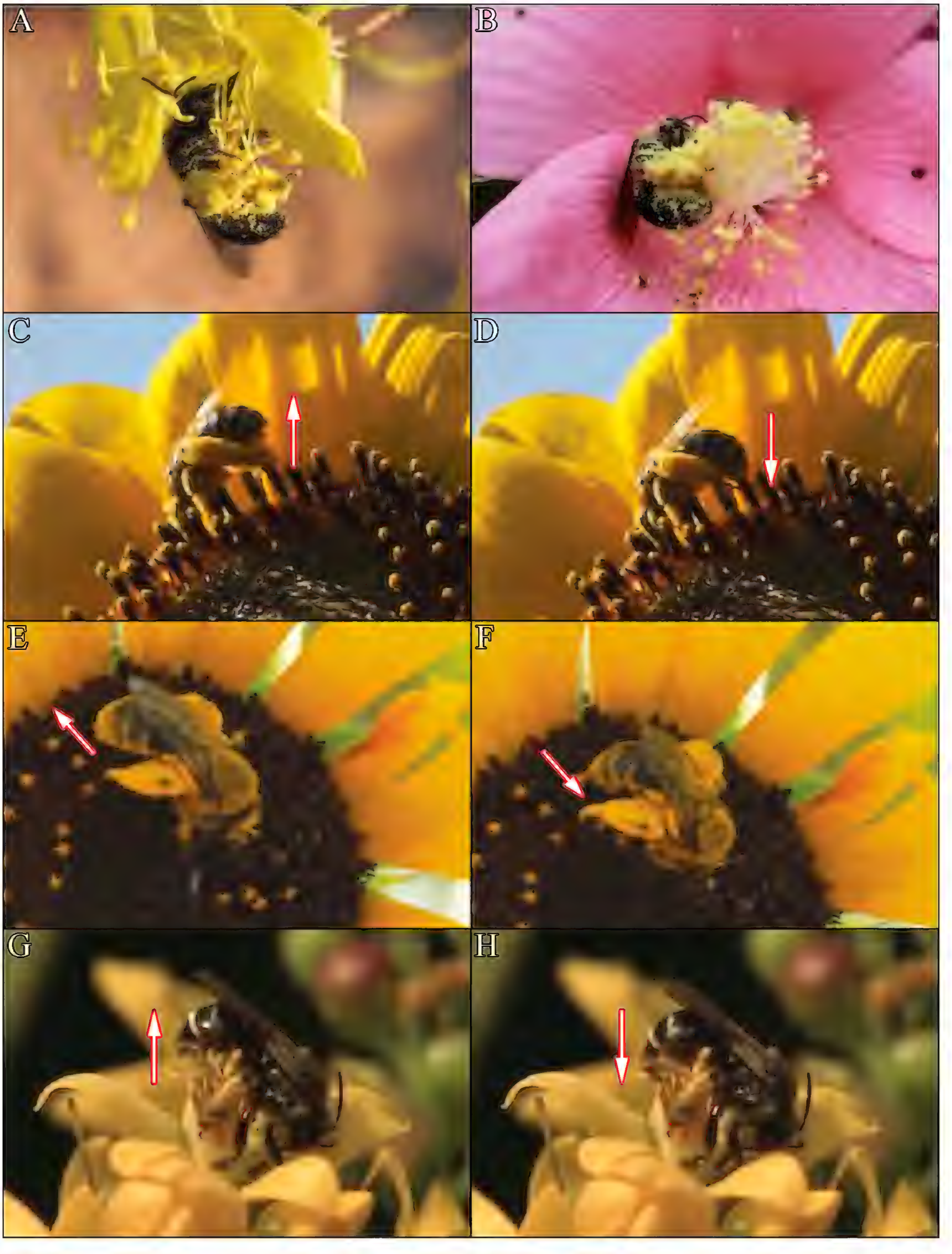

Figure 3. Rubbing with the body and/or scopae. **A** *Andrena* sp. (Andrenidae) rubbing with the abdomen and scopae on *Camissonia* (Onagraceae) **B** *Ptilothrix bombiformis* (Cresson) (Apidae) rubbing with the abdomen and scopae on *Hibiscus* (Malvaceae) **C, D** *Melissodes* sp. (Apidae) rubbing with the abdomen on *Helianthus* (Asteraceae) **E, F** *Andrena helianthi* Robertson rubbing with the abdomen on *Helianthus* **G, H** *Macropis* sp. (Melittidae) rubbing with the venter of the thorax and abdomen on *Lysimachia* (Primulaceae).

diffuse scopa that cover both the ventral abdomen and hind legs (e.g. *Ptilothrix*). Rubbing behavior has been observed in a wide variety of species in every bee family (except Stenotritidae) on numerous floral hosts (Table 2) and is likely more common than the relatively few observations suggest.

Gathering pollen directly with the abdomen and/or scopae has been known since at least the late 1800's though it was not described in detail (Müller 1883; Robertson 1889, 1899; Stephen et al. 1969). Rubbing behavior has been referred to by a wide variety of inconsistent descriptions and terms and has often been referred to as, or lumped together with "tapping," which we consider a separate behavior. As a result, some examples which have been previously referred to as "tapping" fall under our definition of rubbing with the body and/or scopae (e.g. Cane 2017). In addition, observations of the same bee species rubbing on the same plant species often result in quite different descriptions: *Hoplitis anthocopoides* on *Echium vulgare* (Boraginaceae) has been reported as "she vibrates [the abdomen] back and forth rapidly against the anthers while her hind legs also move back and forth against the anthers and scopa" (Eickwort 1973) and alternatively described as "rapidly contracts and expands her abdomen, accordion fashion, over the anthers" (Strickler 1979). Similarly, *Dieunomia triangulifera*, while foraging on *Helianthus annuus* (Asteraceae) has been reported as "waggling the abdomen vigorously from side to side" (Cross and Bohart 1960), as well as "tapping the heads of the disc flowers with the ventral surface of the [abdomen]" (Minckley et al. 1994). We use the term "rubbing" to refer to these behaviors because the term is succinct, accurate, and paraphrases the earliest descriptions, which typically overlap with other more well-known behaviors (e.g. "scraping," "vibrating," and "waggling").

Most bees that gather pollen via rubbing take up the pollen directly with the abdominal scopa (e.g. Megachilidae) or by a combination of the hind leg scopae and abdomen (e.g. *Ptilothrix* and *Andrena* sp. – Figure 3A, B; Suppl. material 3). Rubbing is used by a wide variety of bees that perform additional variants at different speeds. For example, *Melissodes* spp. and *Andrena helianthi* both collect pollen from *Helianthus* by repeatedly rubbing the curled-over apex of their abdomen against the anthers, with the hind leg scopae periodically scraping the abdomen to transfer the gathered pollen (Figure 3C–D; Suppl. material 3). The basic movements of the legs and abdomen of the different species are more or less the same even though the speeds of the abdominal movements can be quite different. Further examples of the variation in rubbing behavior are seen in *Ptilothrix bombiformis* gathering pollen from *Hibiscus* as well as *Andrena* sp. gathering pollen from *Camissonia*, both of which curl the abdomen over a clump of anthers held by the legs (Figure 3A, B; Suppl. material 3). In addition, the venter of the thorax can be used for rubbing in tandem with the abdomen or scopae. Examples include bees in the genus *Macropis*, which use rubbing to accumulate pollen on corkscrew-shaped hairs on the venter of the thorax and abdomen (Cane et al. 1983; Vogel 1992; Schäffler and Dötterl 2011). Despite the variations in movement and speed, all of the aforementioned rubbing variants appear derived from the universal abdominal grooming and pollen-packing movements which involve tamping the legs against the sides and base of the abdomen (Michener et al. 1978), and any attempt to

Table 2. Rubbing with the body and/or scopae in the literature.

Genus or Species	Behavior Description	Floral Host	Citation
Family Andrenidae			
Protoxaea gloriosa (Fox)	Holding the anthers against the abdominal venter and hind legs and shaking them while rotating the body	*Kallstroemia* (Zygophyllaceae)	Cazier and Linsley 1974
Andrena erigeniae Robertson	"pollen was … rubbed from the anthers onto the bee's body and legs"	*Claytonia* (Montiaceae)	Davis and LaBerge 1975
Andrena sp.	Rubbing with abdominal and hind leg scopae	*Camissonia* (Onagraceae)	Figure 3A; Suppl. material 3
Family Apidae			
Eucera (*Tetralonia*) *fulvescens* (Giraud) [as *Tetralonia dufouri* [sic]]	"tummy-tapping"	Asteraceae	Westerkamp 1996
Eucerini spp.	"tummy-tapping"	Asteraceae	Simpson and Neff 1987
Melitoma spp.	"scraping [anthers] with the hind legs"	*Ipomoea* (Convolvulaceae)	Araujo et al. 2018
Ptilothrix bombiformis (Cresson)	"pollen was worked into the scopae"	*Hibiscus* (Malvaceae)	Rust 1980; Figure 3B; Suppl. material 3
Ptilothrix fructifera (Holmberg)	"brush the anthers [between the midlegs, hindlegs, and abdomen]"	*Opuntia* (Cactaceae)	Schlindwein and Wittmann 1997
Svastra obliqua (Say)	"tummy-tapping … with the distal portion of the abdominal venter"	Asteraceae	Simpson and Neff 1987
S. obliqua and *Melissodes agilis* Cresson	"rhythmically tapping … with the distal venter of their slightly decurved abdomen"	Asteraceae	Cane 2017
Family Colletidae			
Perditomorpha brunerii Ashmead	"pollen grains were also scraped directly from the anthers with the scopal setae on the abdominal sterna"	Malvaceae	Gaglianone 2000
Tetraglossula bigamica (Strand)	"rubbing the abdomen against the anthers"	*Ludwigia* (Onagraceae)	Gimenes 1997
Family Halictidae			
Dieunomia triangulifera (Vachal)	"waggling the abdomen vigorously from side to side"	*Helianthus* (Asteraceae)	Cross and Bohart 1960
D. triangulifera	"tapping the heads of the disc flowers with the ventral surface of the metasoma"	*Helianthus*	Minckley et al. 1994
Nomiinae spp.	"tummy-tapping"	Asteraceae	Simpson and Neff 1987
Systropha planidens Giraud	"they rapidly moved their abdomen up and down"	*Convolvulus*	Gonzalez et al. 2014; S. Burrows pers. comm.
Family Megachilidae			
Hoplitis anthocopoides (Schenck)	"she vibrates [the abdomen] back and forth rapidly against the anthers while her hind legs also move back and forth against the anthers and scopa"	*Echium* (Boraginaceae)	Eickwort 1973
H. anthocopoides, *H. producta* (Cresson), *Megachile relativa* Cresson, *Osmia caerulescens* (L.) [as *O. coerulescens* (L.)]	"rapidly contracts and expands her abdomen, accordion fashion, over the anthers"	*Echium*	Strickler 1979
O. lignaria Say, *Megachile* spp.	"filaments are held between the hind legs and … raked against the scopal hairs"	*Collinsia* (Plantaginaceae)	Rust and Clement 1977
Hoplitis simplex (Cresson)	"scrapes pollen directly from the anthers into her abdominal scopa using her hind legs while tapping the anthers with her abdomen"	*Nemophila* (Boraginaceae)	Neff 2009
Ochreriades fasciatus (Friese)	"repeatedly tap their metasomal scopa directly against the anthers"	*Ballota* (Lamiaceae)	Rozen et al. 2015; G. Pisanty pers. comm.
Family Melittidae			
Hesperapis regularis (Cresson)	"scraping [with the scopae]"	*Clarkia*	Burdick and Torchio 1959
H. regularis	"rapid lateral oscillations of the abdomen"	*Clarkia*	Stage 1966
Macropis nuda (Provancher)	"patting motions of the metasoma"	*Lysimachia* (Primulaceae)	Cane et al. 1983
M. fulvipes (Fabricius)	"females pressed the ventral side of the abdomen (by bending) against the anthers"	*Lysimachia*	Schäffler and Dötterl 2011; Schäffler pers. comm.

draw a clear dividing line between these variations will likely become increasingly futile as more observations are made.

Finally, various mentions in the literature suggest that rubbing behavior has been observed in additional species but precise enough descriptions for confirmation are lacking, and many of these could refer to tapping (see next section). This includes suggestions of rubbing by *Osmia lignaria*, *O. indeprensa* Sandhouse, and *O. kincaidii* Cockerell ("the anthers are drawn to the scopal hairs by the hind legs," Cripps and Rust 1989), *Megachile willughbiella* (Kirby) ("the scopa is brushed over the pollen presenting structures," Teppner 2005), as well as *O. bicornis* (L.) [as *O. rufa* (L.)] on *Ranunculus*, and *O. leaiana* (Kirby) and *O. caerulescens* on Asteraceae, which were observed "walking over the anthers so that the ventral scopa touched them while they probed the nectaries" (Raw 1974). In addition, various Megachilidae have been reported to gather pollen by "seesawing" the scopa directly against anthers: *Hoplitis robusta* (Nylander) on *Potentilla* (Rosaceae), *H. zandeni* (Teunissen and van Achterberg 1992), *Osmia* spp. on various hosts, *Pseudoanthidium eximium* (Giraud) on Asteraceae, and *Protosmia minutula* (Pérez) on Lamiaceae (Müller 1996a, 1996b, Müller and Mauss 2016). Lastly, various bees visiting *Clarkia* (Onagraceae) perform a "pollen dance" and "vibrate their bodies laterally" on the flowers and potentially rub their bodies and/or scopae to pick up pollen (MacSwain et al. 1973).

Tapping

Tapping refers to the act of picking up pollen through a rapid up and down motion of the abdominal venter directly against the anthers (Figure 4; Suppl. material 4). It is characterized by the horizontal orientation of the abdomen, the rapidity of movement, and the lack of continuous contact with the anthers (Cane 2017). The term "tapping" comes from what appears to be the original use by Pasteels and Pasteels (1974): "l'abdomen qui tapote de haut en bas sur étamines" ("the abdomen tapped up and down on the stamens"). In the same year, Rust (1974) used "thumping" to describe the behavior. However, Rust subsequently switched to the term "tapping" (Cripps and Rust 1989) to describe the behavior in the same species (Table 3).

Historically, "rubbing" and "tapping" with the abdomen have often been lumped together (e.g. Müller 1883; Simpson and Neff 1987; Westerkamp 1996; Thorp 2000). However, there are distinct differences between tapping and rubbing with the body and/or scopae: in tapping, the rate of movement is faster (Cane 2017), the abdomen is kept more rigid, and the orientation of the abdomen is parallel to the plane of anthers (compared to curled over in typical rubbing). Further, rubbing entails nearly continuous contact, while tapping is characterized by intermittent contact. In rubbing behavior especially, the legs are often used to grab a clump of anthers and rake them against the scopal hairs. Despite these differences, additional exploration of this behavior may reveal that rubbing and tapping fully intergrade, however, until that time, we follow Cane (2017) in splitting these behaviors. Currently, tapping has been observed solely in bees of the family Megachilidae (*Heriades*, *Lithurgus*, *Pseudoanthidium*, *Osmia*, *Megachile*, and *Trachusa*) on asteraceous hosts (Table 3).

Figure 4. *Osmia* sp. tapping on Asteraceae. The directionality of the rapid movement of the abdomen is denoted by **A** down **B** up, and **C** down arrows.

Table 3. Tapping behavior in the literature. All bee species are in Megachilidae.

Genus or Species	Behavior Description	Floral Host (all Asteraceae)	Citation
Heriades spp.	"l'abdomen qui tapote de haut en bas sur les étamines" [the abdomen taps up and down on the stamens]	Asteraceae	Pasteels and Pasteels 1974
Osmia montana Cresson	"a rapid thumping movement of the abdomen"	*Helianthus*	Rust 1974
O. californica Cresson and *O. montana*	"very rapidly tapping the abdominal scopa against the composite disk anthers"	Asteraceae	Cripps and Rust 1989
O. californica	"tamp their abdomens"	*Balsamorhiza, Helianthella, Helianthus*	Williams 2003
Megachile melanopyga Costa and *M. octosignata* Nylander	"rapid up and down movements [of the abdomen]"	*Centaurea*	Müller and Bansac 2004
O. californica	"patting the flowers with their abdominal venters"	*Balsamorhiza*	Cane 2005
Heriades truncorum (L.)	"moving the abdomen rapidly up and down"	Asteraceae	Praz et al. 2008
O. californica and O. montana	"rapidly drumming or patting their abdomens up and down against the pollen-bearing floral styles"	*Balsamorhiza*	Cane 2011
O. californica, *O. coloradensis* Cresson, *O. montana*, *O. subaustralis* Cockerell, *Heriades cressoni* Michener (as *H. cressonii*)	"drumming"	Various Asteraceae	Cane 2017
Heriades crenulatus Nylander, *Lithurgus chrysurus* Fonscolombe, *Pseudoanthidium literatum* (Panzer), *Trachusa dumerlei* (Warncke)	"the rapid movement of their abdomen up and down"	*Centaurea*	Gonzalez et al. 2017; Gonzalez pers. comm.
Wainia eremoplana (Mavromoustakis)	"rapid up and down movements of the metasoma"	Asteraceae	Müller et al. 2018
Osmia sp.	Tapping with the abdominal scopa	Asteraceae	Figure 4; Suppl. material 4

Rubbing with the face

In this behavior, the face (anterior head) is used to gather pollen through direct, continuous rubbing contact with the anthers (Figure 5; Suppl. material 5). Rubbing with the face (reviewed in Müller 1996a; Thorp 2000) is found in numerous unrelated species in the families Apidae, Andrenidae, Halictidae, Megachilidae, and the wasp subfamily Masarinae (Vespidae). In most cases, the hairs on the clypeus and/or frons are thickened, hooked, or corkscrew-shaped, but they can also be unmodified (Müller 1996a; Prosi et al. 2016). Rubbing with the face is associated with the collection of pollen from nototribic flowers, which have the stamens and styles facing downwards from the dorsum of the corolla, thereby promoting contact with the dorsum of floral visitors (Müller

Figure 5. *Osmia pilicornis* Smith (Megachilidae) gathering pollen by rubbing with the face against the anthers of *Ajuga reptans* L. (Lamiaceae). The bee repeatedly jerks the entire body **A** up and **B** down. Image adapted from Prosi et al. (2016).

1996a; Thorp 2000). We follow the terminology of Müller (1996a), who referred to the behavior as "rubbing with the facial area" or "rubbing with the face."

Additional and recent examples of bees with modified facial pilosity that gather pollen from nototribic flowers include *Lasioglossum tropidonotum* McGinley (McGinley 1986); *Osmia brevis* Cresson, *O. cyaneonitens* Cockerell, and *O. ednae* Cockerell on *Penstemon penlandii* W.A. Weber (Plantaginaceae) (Tepedino et al. 1999); *Anthophora walteri* Gonzalez on *Salvia* (Lamiaceae) (Gonzalez et al. 2006); *O. calaminthae* Rightmyer, Deyrup, Ascher, and Griswold on *Calamintha* (Lamiaceae) (Rightmyer et al. 2011); *Megachile riyadhense* (Alqarni, Hannan, Gonzalez, and Engel) seen visiting *Blepharis* (Acanthaceae) (Alqarni et al. 2012); and *O. pilicornis* Smith on *Ajuga* and *Glechoma* (both Lamiaceae) (Prosi et al. 2016). Both *O. calaminthae* and *O. pilicornis* – two species for which detailed observations of pollen gathering are available – rapidly move their heads and bodies up and down against the anthers to remove pollen (Figure 5; Suppl. material 5; Rightmyer et al. 2011; Prosi et al. 2016). Interestingly, *O. pilicornis* also has hooked hairs on the mouthparts, which it uses to scrape pollen from flowers of *Pulmonaria* (Boraginaceae). In some cases, such as in *Rophites algirus* Pérez (Halictidae), rubbing with the face is combined with buzzing (Müller 1996a).

Rasping

Rasping is defined as rubbing anthers with the thoracic dorsum by moving the entire body in and out of the flower, causing vibrations which release pollen (Figure 6; Suppl. material 6). Rasping is a specialized behavior that has only been observed in bees foraging on *Penstemon* flowers that have partially concealed anthers with dentate tips (Table

Table 4. Rasping behavior in the literature.

Genus or species	Behavior Description	Floral Host	Citation
Pseudomasaris vespoides (Cresson) (Vespidae)	"[the anthers] rub against the thoracic surface"	*Penstemon* (Plantaginaceae)	Torchio 1974
Hymenoptera spp.	"the anthers have teeth that rasp against the back and wings of the pollinator"	*Penstemon*	Thomson et al. 2000
Osmia spp.	"the deliberate rubbing of their backs against the anthers"	*Penstemon*	Wilson et al. 2006
O. brevis Cresson	"rasping"	*Penstemon*	Cane 2014

4). Various Hymenoptera – including the pollen wasp *Pseudomasaris vespoides* (Cresson) (Vespidae), and mason bees *Osmia brevis*, *O. pentstemonis* Cockerell, and potentially other *Osmia* species – have been observed rubbing their thoracic dorsum against the dentate anthers to release the pollen (Torchio 1974; Wilson et al. 2006; Cane 2014). Rasping is associated with a roughened or punctate integument on the scutum of *P. vespoides*, which assists in vibrating the anthers (Torchio 1974; Cane 2014). Cane (2014) coined the term "rasping" due to the noise produced by the behavior. This noise was also observed by Torchio (1974), who reported the noise produced as a "clicking" sound. Interestingly, *O. brevis* also collects pollen from *Penstemon* by buzzing (Cane 2014) as well as by rubbing with the face (Tepedino et al. 1999). The different pollen gathering behaviors of *Osmia* on *Penstemon* may be related to the size of the *Penstemon* flowers, with rasping performed in larger flowers and other strategies used in smaller-flowered species (P. Wilson, pers. comm.). So far, rasping has only been observed on *Penstemon* flowers; it remains to be seen whether this pollen gathering is found in additional bee taxa or is performed on other nototribic flowers.

Incidental

When pollen accumulates on a bees body as a by-product of another behavior without any obvious deliberate pollen gathering movements related to that area, it is termed incidental (Suppl. material 7; Doull 1970; Buchmann and Shipman 1990; Thorp 2000). This pollen can either be discarded or packed into the pollen transporting structures (Hodges 1952; Doull 1970). The terms "incidental" and "passive" pollen collection have been used more or less interchangeably in the past (Thorp 2000); "incidental" has been more prevalent historically (e.g. Parker 1926; Doull 1970; Morse 1982) and "passive" has been used more often recently (e.g. Westerkamp 1996; Williams 2003). We prefer the term incidental because it is the earlier accepted term and "passive" implies that the pollen is picked up unintentionally, which is often not the case, since many bees engage in behaviors that appear to maximize the amount of pollen picked up incidentally.

Incidental pollen collection is always a secondary behavior that occurs when a bee performs a primary behavior such as nectar collecting, oil collecting, or another pollen collecting behavior. Incidental pollen gathering is further characterized by the accumu-

Figure 6. *Osmia* sp. (Megachilidae) performing rasping behavior on *Penstemon* (Plantaginaceae). The bee repeatedly jerks the whole body in and out to rasp the anthers, and then uses the midleg to scrape pollen from the dorsum of the thorax upon exiting the flower.

lation of pollen on generalized body hairs rather than specifically on a specialized brush or patch of hairs. This is particularly relevant when incidental buildup occurs during other primary behaviors such as rubbing or tapping, where pollen is incidentally accumulated on non-target areas. The amount of pollen actually picked up depends on the degree of contact with the anthers and the hairiness of the bee (Stavert et al. 2016). That the hairs specifically function to enhance pollen collection seems clear, since cleptoparasitic bees tend to undergo a reduction in overall hairiness along with the loss of their pollen-collecting behavior (Müller 1883; Robertson 1899; Stephen et al. 1969).

A major component of incidental pollen gathering is the degree of movement exhibited by the bee, since the act of moving over or through anthers invariably results in the incidental accumulation of pollen. The degree of movement represents a continuum, encompassing bees that move simply to reach the next anther or nectary and bees that seem to purposefully move as a means to rapidly accumulate additional pollen on their bodies. For example, on open flowers such as *Cornus* (Cornaceae), *Daucus* (Apiaceae), and *Spiraea* (Rosaceae), *Bombus* wade rapidly over flowers with their mid and hind legs and abdomen appressed in a way that maximizes the incidental collection of pollen, although the primary active mode of pollen gathering is still scraping with the forelegs (Heinrich 1976b; Morse 1982). Many different terms have been used to describe the movement of bees on flowers, e.g., "wallow," "run," "wade," "crawl," "sweep," "scramble," "walk," "scurry," "rotate," and "scrabble" (Malyshev 1936; Bohart and Nye 1960; Cross and Bohart 1960; Heinrich 1972; Houston 1975; Heinrich 1976b; Houston and Thorp 1984; Buchmann and Shipman 1990; Thorp 2000). We prefer the term "wade," since it is the earliest term to describe moving over or through a flower that also does not imply a specific speed (Bohart and Nye 1960). In addition, it accurately describes the behavior of how a bee moves both over and through a plane of floral structures.

Most bees appear to use incidental pollen collection to supplement their primary pollen gathering behaviors. For example, many groom off the incidentally accumulated pollen between flower visits and pack it into their pollen transport structures. However, some species appear to collect the majority of their pollen incidentally. For example, *Megachile fortis* Cresson gathers pollen by accumulating it on the body while foraging for nectar (Neff and Simpson 1990), while other species – including bees in the genera *Dasypoda* (Melittidae), *Panurgus* (Andrenidae), and *Protoxaea* (Andrenidae)

– “wallow” in anthers whilst nectaring to gather pollen, though these could potentially refer to rubbing with the abdomen and/or scopae (Malyshev 1936; Linsley and Cazier 1972). Incidental collection of pollen is often used by honey bees and bumble bees, which gather nectar without making any special effort to gather pollen, yet still pack accumulated pollen into the corbiculae (Suppl. material 7; Parker 1926; Hodges 1952; Heinrich 1976b; Morse 1982).

Temporary accumulation of pollen

In addition to the seven main pollen gathering behaviors, temporarily accumulating pollen on a specialized patch of hairs represents an important intermediate step in the pollen gathering behavior of many bee species (Suppl. material 8, Suppl. material 9). Traditionally, most bees are thought to gather pollen with the legs and immediately transfer it to the scopae, or, alternatively, take the pollen which has adhered to generalized body hairs and groom it into the scopae (Michener et al. 1978; Michener 2007). However, many bees perform a third method in which they temporarily accumulate large amounts of pollen onto a discrete patch of specialized hairs before transferring it to the scopae. These specialized hairs are simple (unbranched) rather than plumose and are often hooked or bent apically (Figure 7). The use of a temporary holding area does not appear to be limited to certain flowers, as bees with a temporary holding area collectively specialize on a wide array of floral families and flower types (Table 5). In addition, numerous species use a temporary holding area even though they gather pollen from open flowers such as *Sphaeralcea* (Malvaceae) or *Prosopis* (Fabaceae), meaning that a temporary holding area is not an adaptation to flowers that restrict pollinator movement and make it impossible to immediately transfer pollen to the scopa.

Temporarily accumulating pollen in a specialized hair patch is well-documented in Panurginae (Table 5) and appears to be used by a majority of species in the subfamily. Based on observations on species in the genera *Perdita* and *Macrotera* (Andrenidae), pollen is initially gathered by scraping with the forelegs and mandibles, which immediately load it into the discrete holding area on the venter of the thorax after each scrape. Once a sufficient quantity of pollen has accumulated in the holding area (which typically covers most of the thoracic venter), the forelegs transfer it to the scopae via the midlegs (e.g. Suppl. material 8; Eickwort 1977; Norden et al. 2003).

In addition to panurgines, other bee groups temporarily accumulate pollen but the behavior is not as well-documented. *Trigona* (Apidae) also load the specialized hair patch on the thoracic venter with the forelegs, but appear to transfer pollen to the corbiculae while hovering (Wille 1963; Michener et al. 1978; Renner 1983). Bees in the genus *Macropis* (Melittidae) also accumulate pollen on their venter, but use specialized corkscrew-shaped hairs that cover nearly their entire ventral body surface (Figure 3G–H; Suppl. material 9; Cane et al. 1983; Vogel 1992; Schäffler and Dötterl 2011). However, in this group, the pollen is loaded directly into the temporary holding area via rubbing with the thorax and abdomen. This behavior may have arisen in *Macropis*

Table 5. Panurgine (Andrenidae) bees documented to temporarily accumulating pollen.

Genus or species	Floral host	Citation
Anthemurgus passiflorae (Robertson)	*Passiflora* (Passifloraceae)	Neff and Rozen 1995; Neff 2003a
Calliopsis subalpina Cockerell	*Sphaeralcea* (Malvaceae)	Suppl. material 8
Macrotera mortuaria (Timberlake)	*Arctomecon* (Papaveraceae)	Suppl. material 8
M. opuntiae (Cockerell)	*Opuntia* (Cactaceae)	Bennett and Breed 1985
M. texana Cresson	*Opuntia*	Neff and Danforth 1991
Panurginus polytrichus Cockerell	Polylectic	Neff 2003b
Perdita floridensis Timberlake	*Ilex* (Aquifoliaceae)	Norden et al. 2003
P. gerhardi Viereck	*Monarda* (Lamiaceae)	Miliczky 1991
P. halictoides Smith	*Physalis* (Solanaceae)	Sullivan 1984
P. minima Cockrell	*Euphorbia* (Euphorbiaceae)	Suppl. material 8
P. multiflorae Parker	*Mentzelia* (Loasaceae)	Suppl. material 8
P. octomaculata (Say)	*Solidago* (Asteraceae)	Eickwort 1977
P. sphaeralceae Cockerell	*Sphaeralcea*	Suppl. material 8
P. spp.	*Prosopis* (Fabaceae)	Simpson et al. 1977
Rhophitulus anomalus (Moure and Lucas de Oliveira) [as *Cephalurgus anomalus*]	Malvaceae	Gaglianone 2000

because the legs are simultaneously occupied by dabbing up oil from the flowers (Vogel 1992). The presence of modified hair patches of hooked or corkscrew-shaped hairs on the venter of other bees whose pollen gathering behavior is unknown, e.g. *Monoeca* (Apidae) and various anthiidine bees (Müller 1996b; Michener 2007; Torretta and Roig-Alsina 2016), suggests that this method of temporarily accumulating pollen may occur in a wider variety of bee groups than is generally reported.

Finally, temporarily accumulating pollen in genal hair baskets has been observed in some bee groups, but it is not clear whether these baskets are loaded by directly scraping against pollen or are loaded with the forelegs. This is seen in *Perdita* subgenus *Heteroperdita*, specialists on *Tiquilia* (Boraginaceae) (Portman et al. 2016); *Hesperapis laticeps* Crawford, a specialist on *Mentzelia* (Suppl. material 9); and both species of *Xeralictus* (Halictidae) – *X. bicuspidariae* Snelling and Stage and *X. timberlakei* Cockerell – also specialists on *Mentzelia* (Snelling and Stage 1995).

Flexibility in pollen gathering behavior

The pollen gathering behaviors of bees are not rigid, stereotyped actions performed in isolation. Instead, bees combine different behaviors, mixing and matching them depending on their behavioral repertoires and the morphology of their host plants. The use of different behaviors on flowers with different morphologies has been well-demonstrated in *Apis* and *Bombus*, which will switch between collecting pollen either actively via scraping or incidentally depending on the floral host (Parker 1926; Heinrich 1976b). Another example is found in *Osmia pilicornis*, which uses the proboscis to gather pollen from *Pulmonaria* and rubs with the face on flowers of *Ajuga* and *Glechoma* (Prosi et al. 2016). Using different behaviors on different hosts is also found in specialist bees, such as the Asteraceae specialist *O. montana*, which taps for pollen on most asteraceous flowers, but scrapes with its legs on *Taraxacum* (Cane 2017). More impressively, *O. brevis*

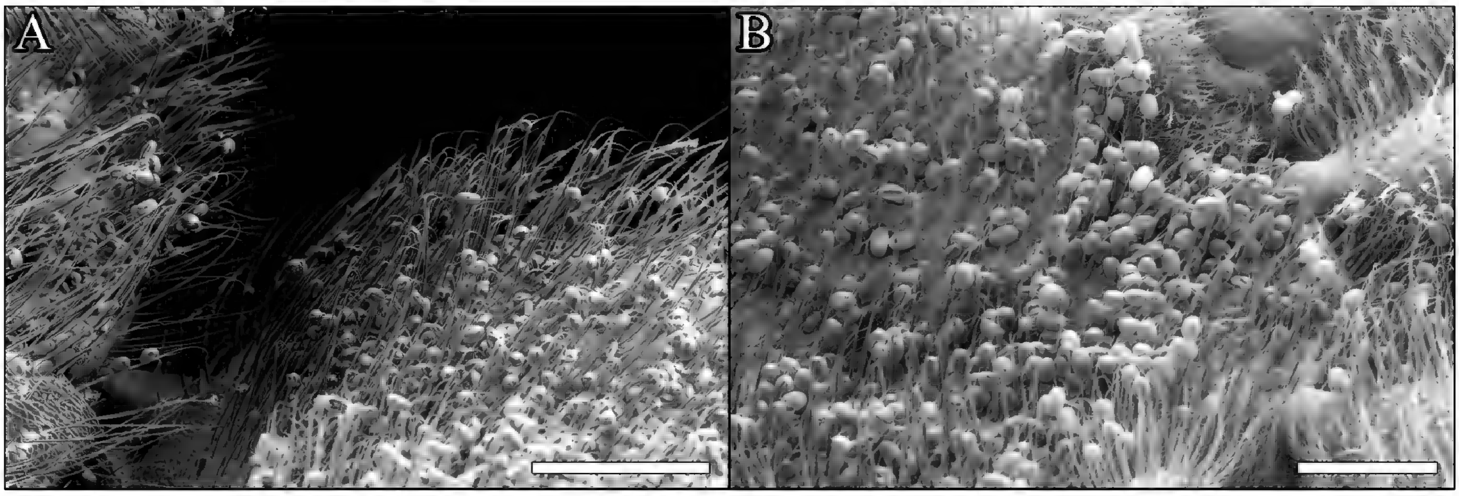

Figure 7. Specialized hairs on the venter of the thorax of **A** *Perdita turgiceps* Timberlake (Andrenidae) with specialized hairs on the fore-coxae (left) and ventral mesepisternum (right) and **B** *Protandrena maculata* Timberlake (Andrenidae) with specialized hairs on the ventral mesepisternum (left) and hind-coxae (far right). Specimens are positioned belly-up, with the head to the left. Scale bars: 200 micrometers.

uses three distinct behaviors when gathering pollen from *Penstemon* – rasping, buzzing, and rubbing with the face (Tepedino et al. 1999; Cane 2014). Another example is seen in *Tetraglossula bigamica* (Colletidae) a specialist on *Ludwigia* (Onagraceae); when anthers are closed, the bees open them with the mandibles and gather pollen by scraping with the fore- and mid-legs. However, when anthers are open, the bees gather pollen by rubbing the scopa directly against them (Gimenes 1997).

In addition to using different behaviors on the same or different hosts, many bees perform multiple pollen gathering behaviors simultaneously. For example, *Andrena helianthi* on *Helianthus* (Figure 3E–F; Suppl. material 3) simultaneously scrapes pollen with the forelegs and rubs the abdomen and scopa against the anthers, and *Osmia* sp. on Asteraceae (Figure 4; Suppl. material 4) taps with the abdomen while at the same time probing for nectar and incidentally picking up pollen on the face and body, which is subsequently groomed into the scopa during flight.

While some bees display flexibility in pollen gathering behavior, others have more limited behavioral suites. One might expect generalist bees to have a broader suite of pollen gathering behaviors than specialist bees. Social bees in particular are expected to be more versatile in their pollen gathering behavior compared to solitary bees because their colonies are active for longer periods and must therefore utilize a broad array of successively blooming plants (Heinrich 1976b). However, this hypothesis does not appear to be well-supported; instead of having a broad breadth of behaviors, many generalists and social bees have relatively limited behavioral repertoires and instead use variations on a small suite of basic behaviors to collect pollen from a variety of different host plants. For example, species in the highly generalist genus *Agapostemon* only use three behaviors: scraping with the extremities, buzzing, and incidental collection (Roberts 1969). Further, *Apis mellifera* and *Trigona* spp. – likely the most generalized bees – are even more restricted, since they do not buzz flowers (Wille 1963; Buchmann 1983). In contrast, the solitary specialist bee *O. brevis* has a much broader suite of behaviors, including scraping, buzzing, face rubbing, rasping, and incidental pollen collection (Tepedino et al. 1999; Cane 2014).

Ecological and evolutionary implications

The repertoire of pollen gathering behavior of bee species may influence their floral host choices. For example, some specialists have limited ability to collect pollen from alternative hosts even though their larvae can develop on alternative pollen sources (Cripps and Rust 1989; Williams 2003). This is particularly apparent in Megachilidae; for example, *Hoplitis anthocopoides* (which rubs directly with the scopa) only gathered pollen from *Echium* (Boraginaceae) and refused to gather pollen from either the related *Anchusa* (Boraginaceae) or alternative hosts in eight other plant families (Strickler 1979). In addition, the Asteraceae specialist *Heriades truncorum* (which taps with the scopa) refused to gather pollen from *Echium* (Praz et al. 2008). Similarly, Williams (2003) observed that the Asteraceae specialist *Osmia californica* (which taps with the scopa) refused to gather either *Phacelia* (Boraginaceae) or *Brassica* (Brassicaceae) pollen when it was the only host present, but, in an interesting twist, did gather some *Phacelia* pollen when its normal asteraceous host was also present. When *O. californica* gathered *Phacelia* pollen, it used the same tapping behavior it used on its normal Asteraceae host, but its attempts were clumsy and inefficient, particularly compared to the more generalized *O. lignaria* (Williams 2003). These examples support the hypothesis that the specialized behaviors of these bees (rubbing or tapping) mean that they are either incapable of gathering non-host pollen or can do so only inefficiently.

In contrast, some other specialist bees readily gather pollen from alternative hosts, particularly in times of pollen shortage (Linsley and MacSwain 1958). For example, an individual of *Diadasia australis* (Cresson) (Apidae), whose normal host is *Opuntia* (Cactaceae), was observed gathering pollen from *Phacelia* after the local cactus blooms were exhausted (Linsley and MacSwain 1958). Another *Diadasia* cactus-specialist, *D. rinconis* Cockerell, was experimentally induced to gather pollen from *Sphaeralcea*, but only after nesting was initiated by the temporary introduction of *Opuntia*, the preferred host (McIntosh 2001). Similarly, *Hesperapis pellucida* Cockerell (Melittidae) was observed gathering pollen from *Gilia capitata* Sims (Polemoniaceae) and other flowers when its normal host, *Eschscholzia californica* Cham. (Papaveraceae), was mowed (Stage 1966). When the normal host recovered and flowered a month later, the bees switched back to gathering pollen from it. *Andrena erythronii* Robertson gathers pollen from *Erythronium* (Liliaceaea) while it is in bloom, but readily switches to other sources once bloom has ended (Michener and Rettenmeyer 1956). Additional *Andrena* species, specialized on *Nemophila*, have also been documented switching to alternative pollen sources when host pollen was in short supply (Cruden 1972). Finally, Thorp (1969) reported multiple species of *Andrena* subgenus *Diandrena* gathering pollen from non-preferred hosts, particularly in times of pollen shortage. All of these bees that readily switch hosts apparently gather pollen primarily by scraping with the forelegs; this generalized pollen gathering behavior could allow them to more easily exploit non-preferred hosts.

Evidence suggests that there is a relationship between pollen gathering behavior and host plant preference. For example, rasping and rubbing with the face are associated with nototribic flowers (Müller 1996a; Table 4), and tapping is associated with

specialization on Asteraceae (Table 3). Similarly, in non-megachilid bees, rubbing with the body and/or scopae is repeatedly associated with floral hosts in the families Asteraceae, Malvaceae, and Onagraceae (Table 2). Plants in those families tend to have more adhesive pollen, either due to sticky viscin threads or spiny pollen with copious pollenkitt (Linsley et al. 1973; Williams 2003; Lunau et al. 2014; Portman and Tepedino 2017). The increased adhesiveness of these pollens may have facilitated the evolution of novel behaviors that take advantage of these pollen properties to efficiently uptake pollen. Particularly if bees have behavioral or morphological adaptations to certain floral or pollen morphologies, this could help explain broad-scale evolutionary patterns of floral host use in bees. This pattern has been repeatedly noted in bee species groups adapted to large or coarse pollen such as in the genera *Diadasia*, *Macrotera*, and *Eucera* (Michener 1944; Linsley and MacSwain 1958; Danforth 1996; Dorchin et al. 2018).

Although some behaviors are associated with particular host plants or floral types, the diversity of pollen gathering behaviors on a given host plant make clear that there is not necessarily a "right way" to gather pollen from a particular host plant. For example, on *Helianthus*, honey bees gather pollen incidentally while nectaring, generalist *Lasioglossum* gather pollen by scraping with the forelegs, *Osmia californica* gather pollen by tapping with the scopae, and *Melissodes* gather pollen by rubbing with the abdomen and scopae. These behavioral differences could potentially be explained by a number of reasons. For example, specialist behaviors such as tapping could be more efficient at particular hosts but less efficient at gathering from alternative hosts (Williams 2003). Conversely, more generalized behaviors could represent a compromise that allows for less efficient utilization of a wider variety of hosts. Lastly, different behaviors on the same host could represent different ecological niches, with some behaviors enabling bees to rapidly skim off accessible pollen while leaving the less accessible pollen untapped, whereas other behaviors could allow bees to meticulously gather the remaining pollen (Simpson et al. 1977).

Conclusion and future directions

Pollen gathering behavior in bees is a complex process that involves the mixing and matching of different behaviors depending on the behavioral repertoire of a given bee species and the floral morphology of host plants. Despite this complexity, pollen gathering can be broken down into two broad categories, "active" and "incidental," with active pollen gathering further divided into six subtypes. In addition, there is an intriguing intermediate step found in disparate groups that involves temporary accumulation of pollen on a discrete patch of specialized hairs. It is our hope that this updated classification of pollen gathering behavior will enable effective communication and comparison of future research, particularly given the rise of low cost, high definition video recording devices.

Despite the abundance of behavioral observations, the breadth and flexibility of pollen gathering behaviors remain poorly understood. Learning more about the behavior

of specific species can help shed light on the evolution of pollen gathering, particularly how behaviors such as rubbing with the abdomen and/or scopa(e), tapping, and rasping evolved and whether they are consistently associated with specific hosts or floral morphologies. Further, it is not clear why some specialist bees have broad behavioral flexibility, while others appear to have much more rigid repertoires. Similarly, it's not clear why some generalists have a smaller breadth of behaviors, particularly the apparent inability of *Apis* and *Trigona* to buzz flowers. Examining the tradeoffs between behavioral breadth and pollen gathering efficiency, as well as the genetic and physiological bases of these behavioral limitations, could shed light on these questions. Towards this end, a comprehensive dataset of the pollen-gathering behaviors of different bee species is needed.

One of the biggest unanswered questions is whether specialized behaviors are more effective at gathering pollen, either by increasing the efficiency of pollen uptake or by allowing bees to perform more than one behavior simultaneously, such as gathering pollen and nectar simultaneously (Strickler 1979). It seems probable that specialized behaviors (e.g. rubbing with the body/scopae or tapping) are more efficient than generalized behaviors (e.g. scraping with the forelegs) on the same host, but this largely remains to be experimentally tested. Conversely, more work is needed to understand whether pollen gathering behavior limits the floral hosts that bees can use.

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Supplementary material 1

Scraping with the extremities

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl1

Supplementary material 2

Buzzing

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl2

Supplementary material 3

Rubbing with the body and/or scopae

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl3

Supplementary material 4

Tapping

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl4

Supplementary material 5

Rubbing with the face

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl5

Supplementary material 6

Rasping

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl6

Supplementary material 7

Incidental pollen gathering

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl7

Supplementary material 8

Temporary accumulation of pollen by panurgine bees

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl8

Supplementary material 9

Temporary accumulation of pollen by melittid bees

Authors: Zachary M. Portman, Michael C. Orr, Terry Griswold

Data type: multimedia

Link: https://doi.org/10.3897/jhr.71.32671.suppl9